[2] Goldschmidt, R., *Zs. ind. Abs.-Vererbungslehre*, **7**, 1912, (1–62); also these PROCEEDINGS **2**, 1916, (53–58).

[3] Called sex intermediates by Riddle; intersexual forms by Goldschmidt.

[4] There is one reference in the literature to androgynous Cladocera (in Daphnia atkinsoni). Judging from De la Vaulx's description these individuals, which he called gynandromorphs, were almost certainly sex intergrades.

[5] Banta, A. M., these PROCEEDINGS, **2**, 1916, (578–583).

[6] The writer used the terms female and male with the mental reservation that inasmuch as femaleness and maleness are now definitely known to be relative in some cases they may be relative in *all individuals* and that the terms female and male are themselves to be considered relative not only in Cladocera, pigeons and moths but perhaps also in all animal and plant forms in which sex is known to occur.

[7] Vaulx, R. de la., *Bull. Soc. Zool. France*, **40**, 1916, (102–104, 194–197,

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ON THE METHOD OF PROGRESSION IN POLYCLADS[1]

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Turbellarians are able to make progress through the water by means of muscular movements of the body as a whole, or of its lateral extensions; their creeping progression on a solid substratum, however, has usually been attributed to the action of cilia. According to Stringer (1917),[2] the locomotion of planarians is effected by muscular contractions, which may be organized after the manner of the locomotor wave upon the foot of a monotaxic gastropod (cf. Parker, 1911),[3] the ciliary activity taking no necessary part in the locomotion. Some observations, which may here be briefly noted, tend to confirm the nature of this finding, and add to the variety of known muscular creeping movements in turbellarians.

One species of Leptoplana, occurring at Bermuda in moderate numbers, differs from the more frequently encountered L. lactoalba Verr., approaching more nearly the form L. lactoalba var. tincta Verr. It is found on the under surfaces of stones, near high water level, and is commonly about 3.5 cms. long. If, out of water, a stone bearing one of these leptoplanas is turned over, exposing the animal to light, it creeps about upon the moist surface. The worm also creeps rapidly under water, and in addition is a vigorous swimmer. It has usually been believed that in Leptoplana "creeping is a uniform gliding movement, caused by the cilia of the ventral surface, aided perhaps [how?] by the longitudinal muscle layer of this surface" (Gamble, 1901, p. 10).[4] While this may very well seem to be the case in L. tremellaris (Gamble, loc. cit.), and in several other species which I have observed, it is distinctly not true of the form which I may refer to as L. 'tincta.' The ventral surface of this platode is richly ciliated, and in creeping it deposits an appreciable slime-track, such as that in which the cilia of triclads have

been supposed to cause creeping owing to their beatings. But the muscular operations involved in the creeping are of so obvious a kind as to be quite unmistakable. These movements are the same whether the worm is in water or out of it, whether it is creeping upon the surface film or on submerged objects.

The essential feature of the progression is illustrated in Figures *A*, *B*, *C*. Creeping is rapid, as quick as 5 mm. per second. One side of the body at the anterior end is lifted from the substratum, thrust 4 to 5 mm. forward, and firmly attached to the substratum; then the opposite side is thrust forward in a similar way. On each side of the body a wave is thus initiated, which may travel the whole length of the animal or may go only one-half to one-third the distance toward the tail. The edge of the body is thrown into wavy wrinkles; these progress toward the posterior end, which is reached in 3 to 4 seconds. The succession of these waves is rapid, so that 4 to 5, or more, may be present at one time on each side of the body. This rapidity makes it difficult, ex-

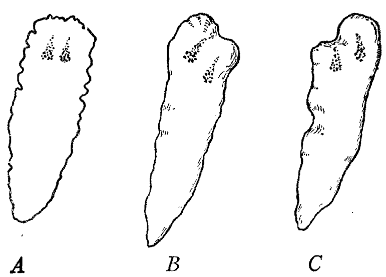

FIG. 1 ILLUSTRATING THE METHOD OF CREEPING IN A SPECIES OF LEPTOPLANA. DIAGRAMMATIC.

A, at rest; *B*, *C*, the initation of alternate waves of body contraction which are responsible for creeping. (Natural size.)

cept at the anterior end itself, to be sure in all cases of the truly alternate relation of the waves on the two sides; but in many instances they undoubtedly remain alternate, especially in slow creeping. The shuffling movement of the worm under these circumstances recalls vividly that of a retrograde alternate ditaxic gastropod foot.[3]

When Leptoplana 'tincta' is induced to creep with special rapidity, the body-waves become more pronounced, and although they remain distinctly alternate and 'ditaxic' in their origin at the anterior end of the animal, they may fuse to form a single retrograde, 'monotaxic' wave after about a third of the worm's length has been traversed. The locomotor wave thus becomes more allied to that developed in swimming, for although some other leptoplanas swim through the water by means of winglike flappings of the lateral extensions of the body,—a process analagous to the parapodial swimming of Aplysia—in L. 'tincta' the swimming movement involves a sinuous longitudinal 'gallop' of the body as a whole.

During progression on a surface, the periphery of the body is the part vitally concerned, for the animal may be transversely arched in such a way that, save at the very anterior end, the periphery is the only part actually in contact with the substratum. The attachment of the peripheral edge of the worm is produced by local suction. Although slime is secreted there, the manner in which the attachment is made to a small surface, e.g., a pencil point, and the way this attachment may be instantaneously released when the worm begins to creep, force one to believe that the edge of the body is not being held in place by sticky slime. This use of the edge of the 'foot' is similar to that found in Chromodoris, and perhaps in other large midibranchs (Crozier and Arey, 1918).[5]

At rest, the outline of L. 'tincta' is usually thrown into 'stationary waves.' These waves may appear truly opposite, not alternate, especially at the anterior end of the worm. Occasionally, at the beginning of creeping, a 'monotaxic' movement is executed, but this operation is characteristically 'ditaxic,' the lateral halves of the body contracting in alternate sequence.

With one of the several species of Pseudoceros which are found inhabiting colonies of the tunicate Ecteinascidia turbinata Herd., I have been able to make observations which show that muscular creeping operations are probably general among polyclads. In this form also the locomotor waves are essentially alternate, 'ditaxic,' and retrograde, the axial region of the body being usually arched away from the substratum, thus separating the body into halves. The wave is a region lifted from the substratum. Two waves may be present on each side, simultaneously. Here, as in the Leptoplana, *when the muscular waves are absent, no creeping progression can be detected.* In the Pseudoceros the waves are especially well seen when the animal is creeping on the surface film. A rippling movement of the outline of the body usually accompanies the 'body-waves,' and when viewed from above this is the only contractile operation to be seen. The peripheral rippling may, however, be very slight or even absent altogether.

Neither of these flat-worms has been observed to creep in any but an anterior direction.

These observations tend to show that in turbellarians generally, muscular operations analagous to those executed by the foot of chitons and of gastropods are essentially concerned in creeping locomotion.

[1] Contributions from the Bermuda Biological Station for Research. No. 89.

[2] Stringer, C. E., 1917, These PROCEEDINGS, **3,** 691–692.

[3] Parker, G. H., 1911, *J. Morph., Wistar Inst., Phila.,* **22,** (155–170).

[4] Gamble, F. W., 1901, *The Cambridge Nat. Hist.,* **2,** p. 1–96, 47 fig., London

[5] Crozier, W. J., and Arey, L. B. *The sensory behavior of Chromodoris zebra.* (In press).